

Dynamics of Darwinian Evolution

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1. **Abstract.** We show that Darwin's theory of evolution implies punctuated equilibria and multiple speciation at the punctuation points. Both phenomena are observed in the fossil record [see for example 11,12,18]. Here *punctuated equilibria* is a term introduced by Gould and Eldredge [9,10], and means that species tend to remain stable for a long time but if one species evolves into another then it tends to do so relatively quickly. Indeed Darwin himself suggests in the *Origin of Species* [1, Summary of Chapter X], "that the duration of each formation is, perhaps, short compared with the average duration of specific forms", and in the later editions he adds "although each species must have passed through numerous transitional stages, it is probable that the periods, during which each underwent modification, though many and long as measured by years, have been short in comparison with the periods during which each remained in an unchanged condition". Hence the fossil record consists of thick layers within which species tend to remain constant, separated by surfaces of discontinuity across which the species change abruptly. We call such a surface a *punctuation point*. By *multiple speciation* at a punctuation point we mean that a single fossil species immediately below that point has given rise to several descendant fossil species immediately above that point, as illustrated in Figure 1. At first sight multiple speciation seems surprising, and it might be thought that a succession of bifurcations as in Figure 2 would be a more "generic" model. For instance successive bifurcations have proved useful in taxonomy. However, if we translate Darwin's actual hypotheses into the simplest possible mathematics, then the latter surprisingly hands us back Figure 1 as the generic situation rather than Figure 2. And it is interesting to note that in the only diagram in the *Origin of Species* Darwin chooses to use Figure 1 rather than Figure 2.

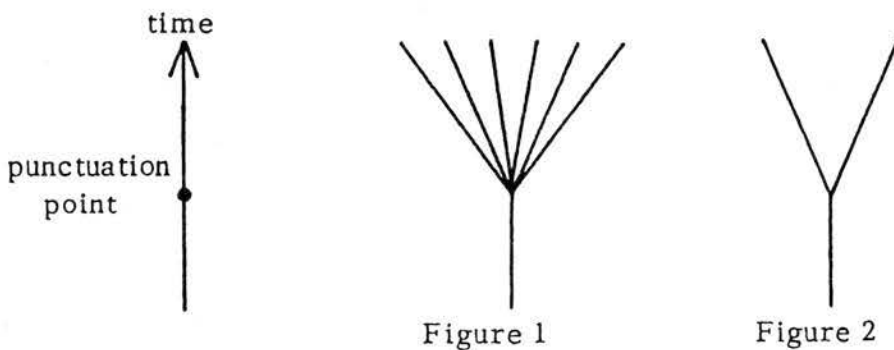


Figure 1

Figure 2

In the mathematical model a species in equilibrium is represented by the minimum of an unfitness function. Introducing parameters to represent a changing environment leads to elementary catastrophe theory, with the catastrophes representing the punctuation points. We use Darwin's original hypotheses to analyse what happens during a catastrophe, and this predicts the multiple speciation. Catastrophe theory has been applied to evolution by a number of authors [including 2,3,4,5,6,7,14,15,17,19,20], but as far as I know this is the first time it has been used to explain the multiple speciation at punctuation points.

Acknowledgement.

I am indebted to many biologists and mathematicians for discussions, particularly Ruth Bellairs, Francis Crick, Maurice Dodson, John Maynard-Smith, René Thom and C.H. Waddington, and I have especially enjoyed the writings of Charles Darwin and Stephen Gould.

2. Darwin's hypotheses.

Darwin's theory of evolution can be summarised briefly as:

- | | | |
|-----------------------------|-------|---------------------------|
| (1) Random small variations | } ==> | (3) Evolution of species. |
| (2) Natural selection | | |

Here (1) and (2) are the slow gradual cause, while (3) is the long term effect. One of the main difficulties of the theory has always been to reconcile the apparent contradiction between the assumed continuity of cause and the observed discontinuities of effect. For instance in the fossil record there are discontinuities in time, and in the living world there are discontinuities in space, and discontinuities of form, to say nothing of the fundamental discontinuity inherent in the very nature of speciation. Darwin was well aware of these problems and devoted a whole chapter of the *Origin of Species* to "difficulties of the theory". His greatest supporter, T.H. Huxley, was also concerned with the problem and even wrote to Darwin the day before the book was published warning him: "You have loaded yourself with an unnecessary difficulty in adopting *Natura non facit saltum* so unreservedly".

As it turns out Darwin and Huxley need not have worried because it is now recognised to be a common phenomenon in science that continuous causes can produce discontinuous effects. The mathematical tool for modelling such phenomena is catastrophe theory, which arises naturally from parametrising functions and ordinary differential equations. The point of view that catastrophe theory emphasises is that (1) and (2) are *local* hypotheses whereas (3) is a *global* conclusion. It is necessary to insert some mathematics, or other types of argument, in between the hypotheses and the conclusion if the latter is to have any meat. Some critics of Darwin complain that his hypotheses are trivial and tautological, and therefore of little scientific use for explanation or prediction. But this mistake arises from looking only at the local point of view; it is analogous to complaining that Newton's law of gravity is trivial because a body twice as massive is obviously twice as heavy, and tautological because if the earth attracts bodies since they fall downwards then it will cause them to fall downwards. In Newtonian theory the critical passage from local to global occurs when passing from the locality of the differential equation to the globality of its solution, and only then does the power and beauty of the theory become apparent in the surprising prediction of elliptical orbits.

Similarly the power and beauty of Darwinian theory only becomes apparent when it is used to explain so many specific and detailed examples of evolution. Such explanations, however, have been primarily verbal rather than mathematical, and I think the reason is that biological measurements tend not to transcend the passage from local to global. Some measurements are local - for instance measuring the fitness of individuals by counting their offspring - and others are global - for instance measuring the means of spindle diagrams of clads to explain the sigmoid nature of the Cambrian explosion [11, Chapter 15]. But those that are both, for instance the size of skull, tend to be descriptive rather than part of a more sophisticated mathematical local-to-global explanation (whereas the measurements in the laws of physics transcend all scales). Therefore if mathematics is going to play any future role in evolutionary theory it is more likely to be qualitative than quantitative [see 19, Chapters 10 and 20]. Furthermore, we may expect it to be useful in precisely those counterintuitive areas where verbal arguments lack conviction, such as when continuous causes produce discontinuous effects.

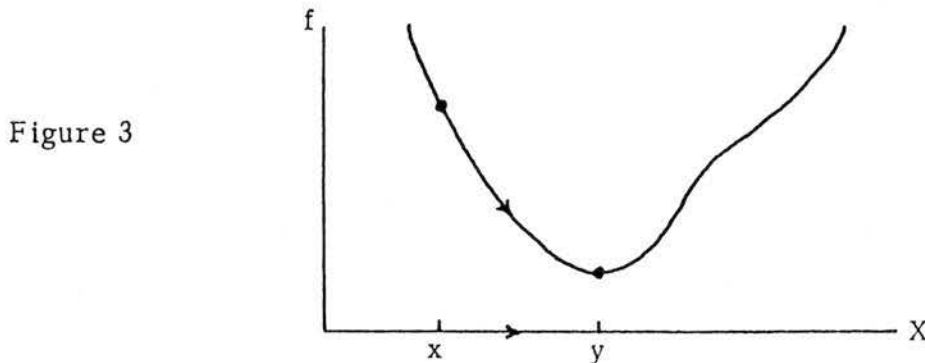
Let us now begin to translate Darwin's hypotheses (1) and (2) into mathematics. Firstly "small variations" suggests representing the individuals of a species by points in a metric space X , the simplest model being n -dimensional

euclidean space (or an open subset thereof). What do the coordinates of X represent? They might be particular significant measurements for the specific example of evolution under consideration, such as length of leg, or the size of beak, or the concentration of some enzyme in some organ, or the timing of some embryological event that affects the eventual shape of the phenotype. We can either confine ourselves to a few explicit variables, or allow ourselves an arbitrary number of implicit variables. Although variations in phenotype must ultimately arise from variations in genotype which are of a combinatorial nature, nevertheless in most cases a continuous model is adequate, and in many cases better, for describing variations in phenotype. Also it is the phenotype rather than the genotype that we want to model, because natural selection acts on the phenotype.

If we want to model the evolution of a symbiotic relationship, or a prey-predator relationship, or an ecology, then we can use the same model with a point in X now representing the symbiotic pair, or the prey-predator pair, or the entire ecology.

We translate the word "random" into mathematics by assuming that the offspring of an individual x will lie in a neighbourhood of x . In Appendix 1 we make that concept more explicit.

Darwin's hypothesis (2) of natural selection means that more offspring are produced than can survive, and so only those more fitted to the given environment will survive. The simplest way to translate "fitness" into mathematics is to postulate an *unfitness function* $f: X \rightarrow \mathbb{R}$, where \mathbb{R} denotes the real number, and $f_x < f_y$ means x is fitter than y . (We use *unfitness* rather than *fitness* in order to exploit the intuition of a ball rolling downhill). Let us postpone discussing the existence and measurability of f until we have begun using it, because then the usage will indicate what needs to be discussed.

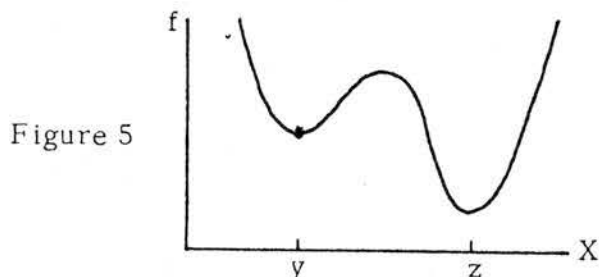
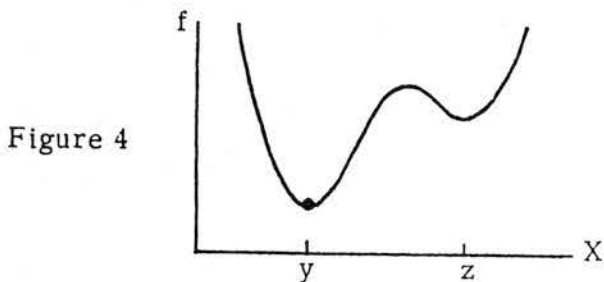


For simplicity suppose at first that X is 1-dimensional, and consider the graph of f as in Figure 3. (At the back of our minds we continue to think of X as n -dimensional, and later it will be important to have X at least 2-dimensional). Suppose that the individuals of a species have mean x , and are clustered in a neighbourhood of x . By hypothesis (1) their offspring will be spread over a slightly larger neighbourhood, and by hypothesis (2) only the fitter will survive, and so the mean of the survivors will be slightly downhill from x . Hence the species will evolve downhill towards the minimum y of f . When the species reaches that minimum then it stabilises, because then any small variations will be less fit and so will not survive. Notice that a minimum of f is already a global concept and so we have already begun the passage from local to global.

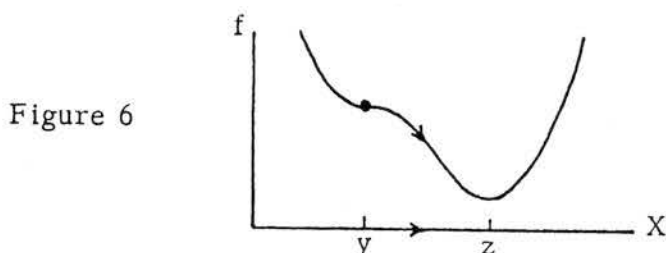
It is tempting to think of evolution as a dynamical system analogous to the ordinary differential equation $\dot{x} = -\nabla f$, but we shall see in §5 that if $\dim X \geq 2$ it obeys a rather different kind of dynamics.

3. Discontinuity in time.

We now introduce the notions of catastrophe theory [2,14,19]. Suppose the environment is gradually changing so that another ecological niche appears at z , as in Figure 4. More precisely we assume that the fitness function gradually changes so as to create a new minimum at z , which represents the form of phenotype best fitted to fill the new ecological niche. Even if this niche gradually becomes more advantageous than y , with a lower minimum as in Figure 5,



the species is prevented from evolving to z because it cannot climb over the intervening hump: any small random variation of individuals towards z is immediately stamped out because they are less fit than the existing population at y . This situation persists until the gradual change in f causes the minimum at y to coalesce with a maximum, as in Figure 6. Now any small random variation toward z will be advantageous, and so the species will evolve until it reaches



z , where it will stabilise again. Compared with the periods of stability previously spent at y , and subsequently spent at z , the time taken to go from y to z is likely to be relatively short, perhaps as little as one thousandth as long as the periods of stability. Hence on the geological time scale it will appear as a catastrophic jump, or more briefly a *catastrophe*. In the fossil record the catastrophe will occupy only a thin surface layer of perhaps one thousandth the thickness of the layer below containing fossils of y , and the layer above containing fossils of z . Such a layer is likely to be so thin that it may not contain any fossils of the intervening forms between y and z , and hence will appear as a surface of discontinuity. Thus we have shown that *Darwin's two local hypotheses imply punctuated equilibria*.

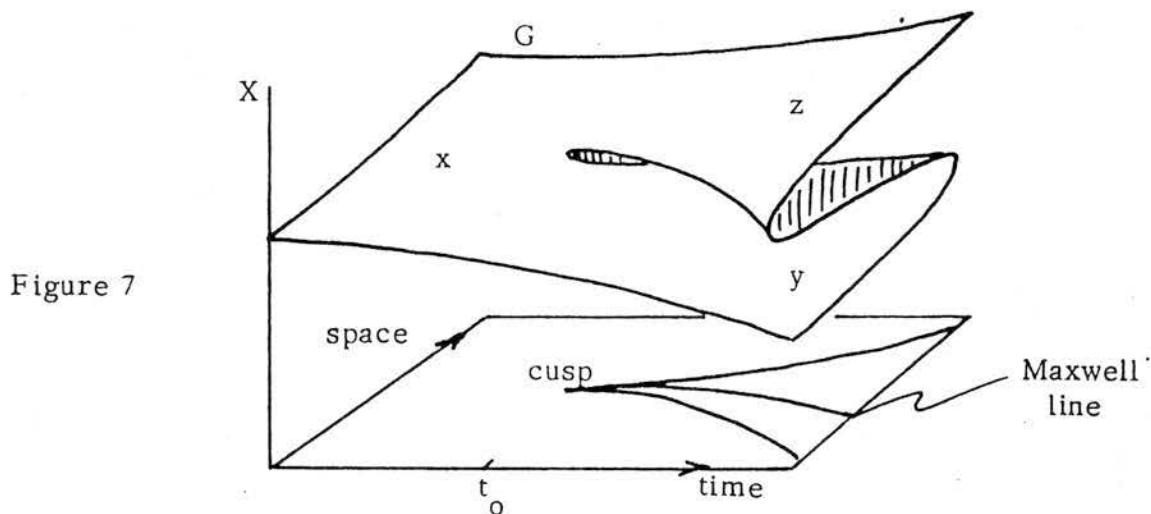
Before leaving the concept of fitness notice that it is really a local ordering rather than a global function. Here *local ordering* means that if we try and measure fitness then we can only really compare two individuals or two types of individual who are relatively close, living at the same time in the same environment at the same place, and order them by saying one is fitter than the other. By contrast, in the above argument we have assumed fitness to be a global function f . Furthermore we have assumed f to be constant during the catastrophe from y to z , or more precisely that the catastrophe is much faster than the gradual rate of change of f . Although the catastrophe is fast on the geological time scale, it may involve as many as 10,000 generations over a time span of 250,000 years. This raises the problem: how can we compare the fitness of y and z , when y is an individual of a totally different shape living 250,000 years earlier than z ? The answer is that we must use mathematics to bridge the gap, and in Appendix 2 we state a theorem proving the existence of the global function,

given the local ordering. A consequence of this existence theorem is that the quantitative value of f is not globally significant: for example we may just as well replace f by ef , where $e: \mathbb{R} \rightarrow \mathbb{R}$ is any increasing function. Therefore it is only valid to use the *qualitative* global properties of f (namely those also shared by ef) of which the most striking are the catastrophes.

4. *Discontinuity in space.*

A gradually changing spacial environment can lead to abrupt frontiers between different but related species occupying the same ecological niche. In the *Origin of Species* Darwin draws attention to several living examples going up mountains, or down oceans, or towards cooler latitudes. In the chapter on the difficulties of the theory he argues how intermediate species might be eliminated, but does not explain how a frontier might form in the first place. We shall show that the cusp catastrophe offers a simple explanation as follows.

The two parameters are space and time, where *space* is 1-dimensional, and refers to the direction in which the spacial environment is changing, and *time* refers to the long-term evolutionary time scale. Suppose that initially a single species x occupies the whole space. Suppose that conditions at one end of the spacial axis favour the gradual evolution of x into a species y , while the other end favours the gradual evolution of x into z . Both evolutions are assumed to be gradual, involving no catastrophes. Assume that the corresponding parametrised fitness function f is smooth, generic, and as simple as possible (i.e. has fewest possible singularities). Then the graph G of minima of f over the parameter space will be as shown in Figure 7 [see 19, Chapter 4]. We have drawn X as a

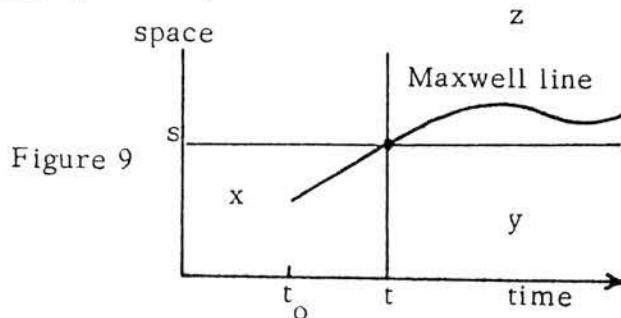
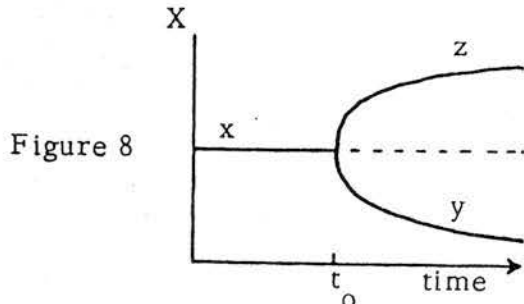


1-dimensional vertical axis, but even if X were n -dimensional the graph G would still be 2-dimensional as shown. The shaded area of G represents maxima of f if $\dim X = 1$, or saddles of f if $\dim X > 1$. For parameter points outside the cusp f will be unimodal, with a unique minimum (as in Figure 3). For parameter points inside the cusp f will be bimodal, with two minima at y and z (as in Figure 4 and 5). Which of the two species is fitter will depend upon which minimum is lower. The fitter species will then dominate at that particular space and time, and take over the ecological niche by eliminating the other species.

Define the *Maxwell line* to be the set of parameter points where the two minima are at the same level. Then the Maxwell line will represent the observed frontier between the two species y and z . Thus we have explained the formation of frontiers.

We can make two further predictions concerning the Maxwell line. Firstly Figure 8 shows that the graph of the species over the Maxwell line is a typical pitchfork bifurcation. Therefore the two species diverge most markedly

immediately after t_0 , the time coordinate of the cusp point, which is the moment when the frontier first appears. Secondly, Figure 9 illustrates the fact that generically there is no reason why the Maxwell line should be parallel to the time axis. Nor is there any reason why it should stabilise parallel to the time axis after some time (unlike the stabilisation of a frontier between two tissues in embryology [19, Chapter 4], which is a bifurcation phenomenon rather than a Maxwell phenomenon). Therefore there are likely to be relatively long periods where one of the species is gradually invading the territory of the other. At any given time t the Maxwell line represents the frontier between the territories of y and z as indicated by the vertical line in Figure 9; and at any given place s the Maxwell line represents a discontinuity in the fossil record between y and z as indicated by the horizontal line in Figure 9.



Dodson [4] describes further applications of catastrophe theory to phenomena involving two spacial dimensions, for example using a cusp to explain how the two overlapping ends of a continuous circular cline may not be able to interbreed.

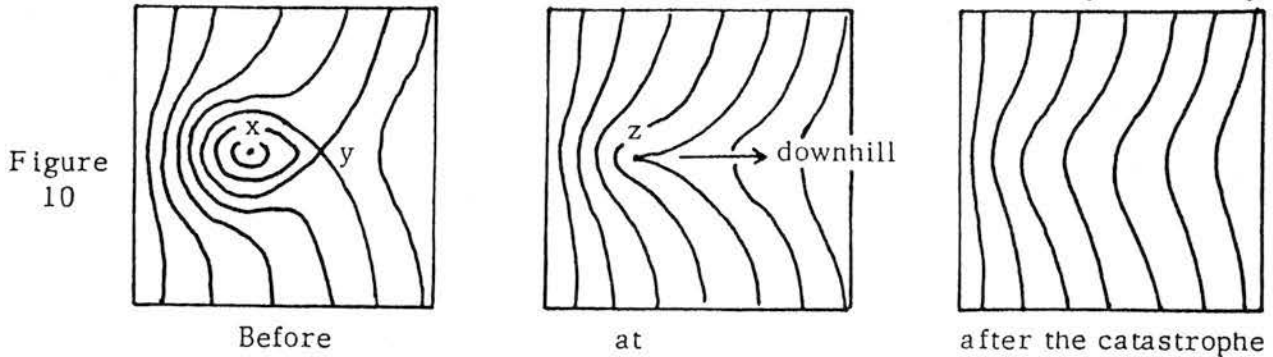
Before leaving spacial discontinuities let us contrast the difference between the catastrophe model here and the conventional explanation of allopatric speciation [6,11]. Allopatric speciation requires the additional and perhaps somewhat artificial hypothesis of a peripheral subset of the species becoming spacially separated from the main body, evolving in isolation, and then reinvading the main territory of the main body. By contrast the catastrophe model only assumes the gradual evolution of the main body within its own main territory. In the allopatric speciation model the separation and spacial discontinuity is a *hypothesis*, whereas in the catastrophe model it is a *conclusion*, deduced from continuous hypotheses.

5. Discontinuity of form.

The most fundamental discontinuity in evolution is speciation, in other words the discontinuity of form. At first sight the lack of intermediate forms between two species, for example between man and chimpanzee, can easily be explained by saying there is a continuity of form in space-time if we backtrack both species to their common ancestor. However, this only localises the problem as to why the common ancestor should have bifurcated in the first place (without introducing some spacial parameter as in the last section). Indeed if the common ancestor were sitting at some minimum of f , then Darwin's hypothesis (2) of natural selection would keep it there, and actively prevent bifurcation. Therefore speciation cannot occur at a minimum of f . Moreover the main classification theorem of elementary catastrophe theory [14,19] implies that since time is 1-dimensional it is in general impossible for a minimum to bifurcate without a catastrophe. Therefore speciation must occur during the catastrophes.

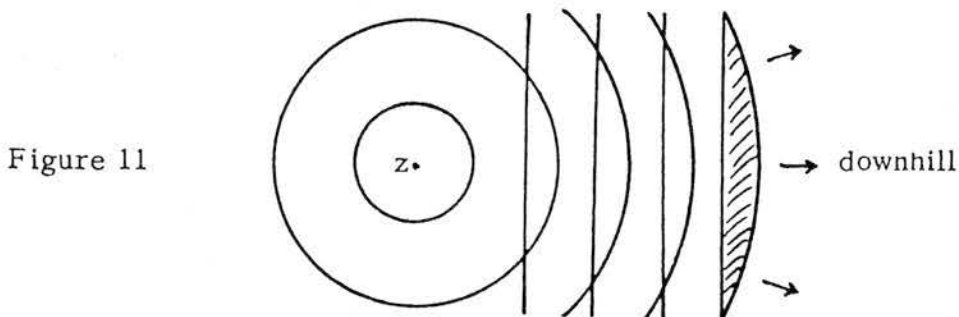
Figure 6 gives no insight into how speciation could occur during a catastrophe because X is only 1-dimensional. To gain the correct insight we must have X at least 2-dimensional, and so we shall imagine X to be a horizontal plane, and f to be the height function of a landscape. Any catastrophe must be triggered by the disappearance of a minimum, or more precisely a gradual change of f causing the coalescence of that minimum with a saddle. This can be visualised as a pond on a

hillside, whose edge is gradually eroding away until it disappears. The generic pictures of the contours of f before, at, and after the moment of catastrophe are shown in Figure 10. Before the catastrophe the species is in stable equilibrium at the minimum x , and y is the saddle point. At the moment of catastrophe x coalesces with y at the point z . The contour through z is a cusp whose interior axis points downhill, and therefore the species begins to evolve specifically in



this direction. When the species starts going further downhill the direction of evolution is not so clear, and to determine what happens it is necessary to go back to Darwin's original hypotheses (1) and (2). According to hypothesis (1), the random small variations will cause the species to spread like a wave in all directions, along the contours as well as downhill. Meanwhile the natural selection of hypothesis (2) will prevent it from going uphill, and by eliminating the less fit will cut off the back of the wave along a contour line. Therefore the species will travel like a solitary wave going downhill at the same time as elongating itself along the contours.

Let us first consider the artificial special case of parallel contours, and equal speeds of variation in all directions. At any given time the species will occupy the sector of a circle as illustrated by the shaded area in Figure 11. As time progresses the radius will increase and the sector will approximate to a strip between two neighbouring contours.

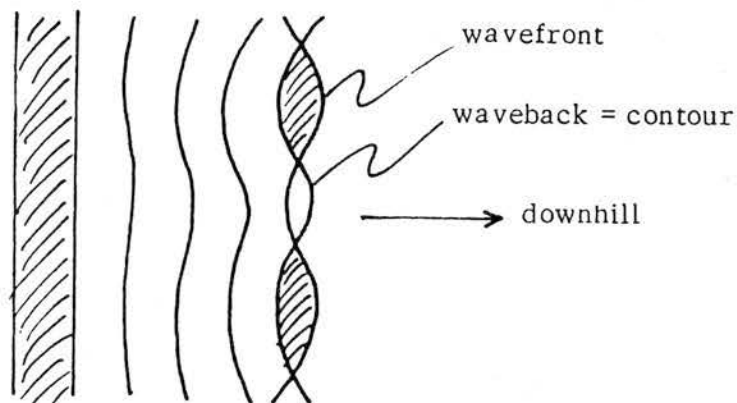


Darwin makes some pertinent comments in his initial chapter on the breeding of domestic species in the *Origin of Species*. A wild breed is stable but "when the organisation has once begun to vary, it generally continues to vary for many generations". Once variation has started "the whole organisation seems to have become plastic".

In general there will be severe problems in measuring the rates of variation and natural selection in terms of measurements of the phenotype. But in any case we would not expect the contours of f necessarily to be parallel, nor the speed of variation necessarily to be the same in all directions. So let us consider what will happen if the contours develop some curvature as shown in Figure 12. Although the value of f will not be significant, as explained in §3, nevertheless the slope $|\nabla f|$ of f may have some significance because it is a local property related to the advantage of increasing fitness. In Appendix 1 we give arguments to suggest that the speed of evolution, in other words the speed of the wave-front downhill, at least for double-sex species, is locally proportional to the slope of f . This implies that where the contours are closer together the speed will be

faster and the wave-front will surge ahead, while the wave-back will lag behind as shown in Figure 12 because it is a contour line. Therefore the species which initially occupied the continuous strip on the left will divide into separate components on the right; individuals in between the components will have been eliminated by natural selection. Moreover the concave curvature of the contours has the effect of "focusing" each component into a relatively small droplet, in other words a well-defined subvariety of the species.

Figure 12



We have drawn X as 2-dimensional and hence the contours as 1-dimensional, but in fact X will really be n -dimensional, and contours $(n-1)$ -dimensional. Therefore the continuous $(n-1)$ -dimensional disc indicated by the shaded strip on the left of Figure 12 is liable to break up into several droplets. Hence the species will break up into several different subvarieties. Initially all these sub-varieties will still belong to the same species, but as they evolve further they will lose the capacity to interbreed and will therefore become separate species. Each will then stabilise as it reaches its own particular minimum of f . Thus multiple speciation will occur during the catastrophe. We have explained *the multiple speciation at the punctuation points* (as in Figure 1).

Before leaving the model notice two further consequences of the focusing effect of the curvature of the contours. Firstly it reinforces the initial direction of evolution shown in the middle diagram of Figure 10; therefore initially all individuals will begin to evolve in the way. Secondly it explains the phenomenon of *canalisation* [16], namely the convergence of phenotype in spite of divergence of genotype. Recent measurements have shown a surprising amount of genetic variability within the same phenotype [8,13].

Appendix 1. The catastrophe wave.

We shall very crudely estimate the size and speed of the wave during the catastrophe, given the mutation rate and fitness advantage. For simplicity assume that the contours of f are parallel and that the wave is constant along contours (neglecting the end effects). Therefore we are only interested in the distribution of populations along the direction x of greatest slope, perpendicular to the contours.

Let P = distribution of parents
 Q = distribution of offspring
 S = distribution of survivors.

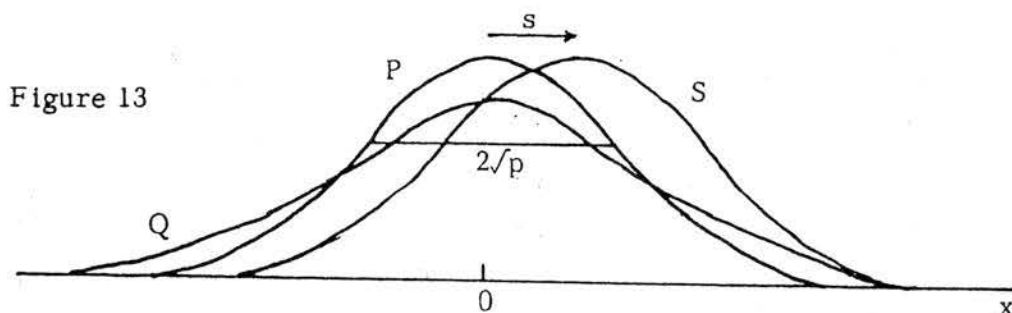


Figure 13

Choose the origin at the mean of P, and for simplicity assume P symmetrical in x. We translate Darwin's original hypotheses (1) and (2) into mathematical hypotheses determining the transformations $P \rightarrow Q \rightarrow S$, as follows.

Hypothesis (1): $P \rightarrow Q$. *Case (a) Single sex.*

Define $Q(x) = \int P(y)N_{\mu}(x-y)dy$, where $N_{\mu} = \frac{1}{\sqrt{2\pi\mu}}e^{-\frac{x^2}{2\mu}}$.

Here μ is a parameter measuring the rate of mutation: offspring are distributed normally about their parent y with variance μ .

Case (b) Double sex.

Define $Q(x) = \iint P(y)P(z)\int_0^1 N_{\mu}(x-((1-t)y + tz)) dt dy dz$.

Here offspring are distributed normally about every point on the interval between their parents y and z. In each case it follows that Q is a symmetric probability distribution with zero mean, like P.

Hypothesis (2): $Q \rightarrow S$. Define $S(x) = (1+\alpha x)Q(x)$.

Here α is a parameter measuring the advantage of increasing fitness as x increases. S is a probability distribution because Q has zero mean.

Hypothesis (3). $\alpha/\mu \ll 1$.

This hypothesis means that, since $\sqrt{\mu}$ is the standard deviation of an offspring from its parent, even if the offspring mutates in the most advantageous direction it can only expect to be marginally fitter than its parent. In other words there is only a small increase in fitness in each generation, which is a translation into mathematics of the word "small" in Darwin's original hypothesis (1).

Hypothesis (4). $S(x) = P(x-s)$.

This hypothesis says that S is a translation of P by distance s, implying that successive generations form a stable travelling wave. We interpret s as a measurement of the speed of the wave.

Let p denote the variance of P, which we can interpret as a measurement of wavelength. (More precisely the "length" of the wave might better be described as $2\sqrt{p}$, as shown in Figure 13, but for convenience we shall use p). We can now calculate the wavelength p and speed s in terms of the mutation μ and advantage α .

Theorem.

Case	p	s
(a)	$\sqrt{\mu}/\alpha$	$\sqrt{\mu}$
(b)	3μ	$3\alpha\mu$

Proof. Let q denote the variance of Q. From hypothesis (1) we can calculate q in the two cases.

$$(a) \quad q = p + \mu \qquad (b) \quad q = \frac{2}{3}p + \mu$$

$$\text{From hypothesis (2), } \begin{cases} s = \text{mean } S = \alpha q \\ \text{variance } S = q - s^2 \end{cases}$$

By hypothesis (4), variance S = p.

$$\text{In case (a), } \quad p = q - s^2 = p + \mu - s^2 \qquad \therefore s = \sqrt{\mu}$$

$$\therefore q = \frac{s}{\alpha} = \frac{\sqrt{\mu}}{\alpha}$$

$$\therefore p = \frac{\sqrt{\mu}}{\alpha} - \mu = \frac{\sqrt{\mu}}{\alpha} \quad (\text{ignoring } \mu, \text{ since } \mu \ll \frac{\sqrt{\mu}}{\alpha} \text{ by hypothesis (3)})$$

In case (b),

$$p = q - s^2 = \frac{2}{3}p + \mu - s^2.$$

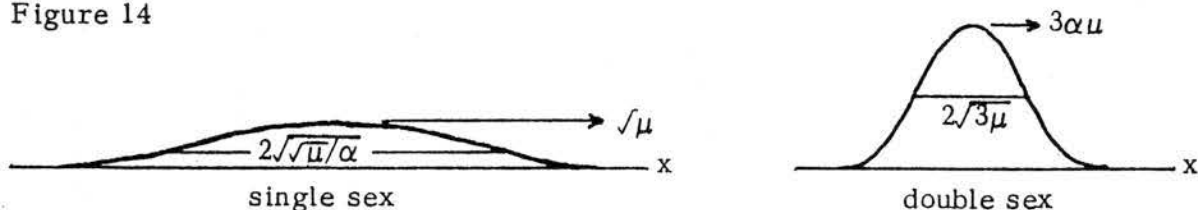
$$\therefore p = 3(\mu - s^2) < 3\mu \quad \therefore q = \frac{2}{3}p + \mu < 3\mu. \quad \therefore s = \alpha q < 3\alpha\mu.$$

$$\therefore s^2 < 9\alpha^2\mu^2 \ll \mu, \text{ by hypothesis (3).}$$

$$\therefore p = q = 3\mu, \text{ ignoring } s^2 \text{ compared with } \mu.$$

$$\therefore s = \alpha q = 3\alpha\mu.$$

Figure 14

**Summarising.**

The single sex wave is shallow and fast, while the double sex wave is high and slow. Therefore the double sex species is more well-defined during catastrophe. The single sex wave travels with the maximum speed that mutation will allow, independent of the advantage, and the advantage only affects the wave length; the more advantageous the shorter the wavelength. The double sex wave has wavelength independent of the advantage, and of the same order as mutation, while the speed is proportional to the advantage. The latter result was useful for the argument about speciation in §5.

Appendix 2: Globalisation of fitness.

Let X be a simply-connected n -manifold. Let F be an oriented foliation on X of codimension 1. Assume that X can be covered by a finite number of basic neighbourhoods for the foliation. Assume that there is no closed curve in X transverse to the foliation.

Theorem. *There exists a function $f: X \rightarrow \mathbb{R}$ whose level curves contain the leaves of F , and which induces the orientation of F and maps paths transverse to the foliation homeomorphically.*

In the application X might be an open neighbourhood in the space of phenotypes of the path of some catastrophe. A basic neighbourhood of the foliation represents a set of individuals living at roughly the same time in the same environment at the same place, and sufficiently close for their fitness to be compared. Individuals of equal fitness determine a local leaf of the foliation of this neighbourhood, and any local measurement of fitness determines an ordering of local leaves, $x < y$ if x is fitter than y , and hence the orientation of F . The finiteness assumption of basic neighbourhoods comes from the finiteness of space and time on earth. The assumption about closed curves comes from the unreasonableness of evolving in a circle getting fitter and fitter. The simply-connectedness assumption comes from the unreasonableness of evolving into exactly the same species by two different routes. Simply-connectedness is a necessary hypothesis for the theorem, because the following counter-example on an annulus satisfies all the other hypotheses but not the theorem.

Figure 15



The conclusion about transverse paths guarantees that f behaves nicely locally, separating the local leaves in each basic neighbourhood, and that f strictly decreases along all evolutionary paths.

The theorem is proved by showing the space of leaves to be an oriented simply-connected, in general non-Hausdorff, 1-manifold. Identifying non-Hausdorff points makes it into a finite oriented tree, which, by induction on edges, can be mapped into \mathbb{R} , embedding each edge and preserving the orientation.

The theorem can be generalised to foliations with singularities. Here a *singularity* means a basic neighbourhood for the foliation foliated by the level curves of a generic germ, where generic means a Morse function or an elementary catastrophe [14,19]. In the application we can therefore include the beginning and end points of a catastrophe.

Since continuous functions can be approximated by smooth functions, and generic functions are open dense in the latter, we may assume that fitness functions are smooth and generic.

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